SIEVE-ELEMENT CHARACTERS OF *TICODENDRON*[1]

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Abstract

Among the families of Hamamelidae, *Ticodendron incognitum* Gómez-Laurito & Gómez P. contains S-type sieve-element plastids, the specifics of which (diameter and starch grains) would place it within or close to Betulaceae/Corylaceae. The absence of persistent, nondispersive P-protein bodies in the sieve elements of *Ticodendron* excludes the families of the Urticales and the Fagaceae, all regularly containing persistent P-protein bodies, from the list of its closest relatives.

Sieve-element characters, i.e., information obtained with the transmission electron microscope on sieve-element plastids, phloem proteins, and other morphological features, have largely been used to delimit higher taxa within angiosperms (Behnke, 1981a), but in a few cases were also helpful to assign single genera to a family (*Lophiocarpus*: Behnke, 1974; *Halophytum*: Hunziker et al., 1974; *Hectorella*: Behnke, 1975; *Swartzia*: Behnke, 1981b; *Geocarpon*: Behnke, 1982).

The hitherto unknown taxonomic position of the newly described genus *Ticodendron* (Gómez-Laurito & Gómez P., 1989a, b) and its probable relationships to various families of the Hamamelidae prompted an investigation of its sieve-element characters. Moreover, a survey of the sieve-element characters of all of the hamamelidaean families (Behnke, 1989) both facilitates a comparison with and asks for a complementation by data from *Ticodendron*.

Material and Methods

Shoot parts of a sapling of *Ticodendron incognitum* were collected in Costa Rica (*Bello & Haber 9809*), divided with a razor blade into longitudinal sections, and immediately immersed into a fixative containing paraformaldehyde and glutaraldehyde (Karnovsky, 1965). The samples were mailed to the author's laboratory, placed for 3 hr. in fresh Karnovsky's fixative, washed with 0.1 M sodium cacodylate buffer, postfixed for 1 hr. in 1% buffered OsO_4, dehydrated in acetone, embedded and polymerized in an Epon-Araldite mixture, and processed according to standard methods for ultrathin sectioning and eventual photographing with a transmission electron microscope.

Part of the prefixed material was dehydrated with ethanol, embedded into histowax, sectioned with a sliding microtome, stained with resorcin blue, and screened with a light microscope.

General Description of the Shoot

Transverse sections of the shoot sample studied show its composition as follows (cf. Figs. 1–3): the innermost part is occupied by the pith (Fig. 1: Pi) containing thin-walled parenchyma cells and large marginal, shizogenous secretory sacs surrounded by six epithelial cells (Fig. 1: o). The length of these sacs, however, is restricted to about three to five times their width. The outermost pith cells, i.e., those bordering the xylem, often have lignified cell walls.

The xylem, phloem, sclerenchyma, and cortex make up distinct layers proceeding toward the periphery of the section. The shoot is protected by a periderm four to six cells broad (Fig. 1: Pe). The presence of a periderm, as well as the extent and the arrangement of xylem and phloem, demonstrate that this shoot part is already in its secondary growth period. The xylem (Fig. 1: X) shows a strict radial arrangement of its rather small and evenly sized cells interspersed by vessels, which may be twice as broad as the other elements but do not greatly disturb the radial array (Figs. 2, 3: X). Small multiseriate rays, in cross sections only one cell broad, are found at regular intervals. In a few parts of the studied shoot sample, the phloem (Figs. 1, 2: P) reflects its origin from radially aligned

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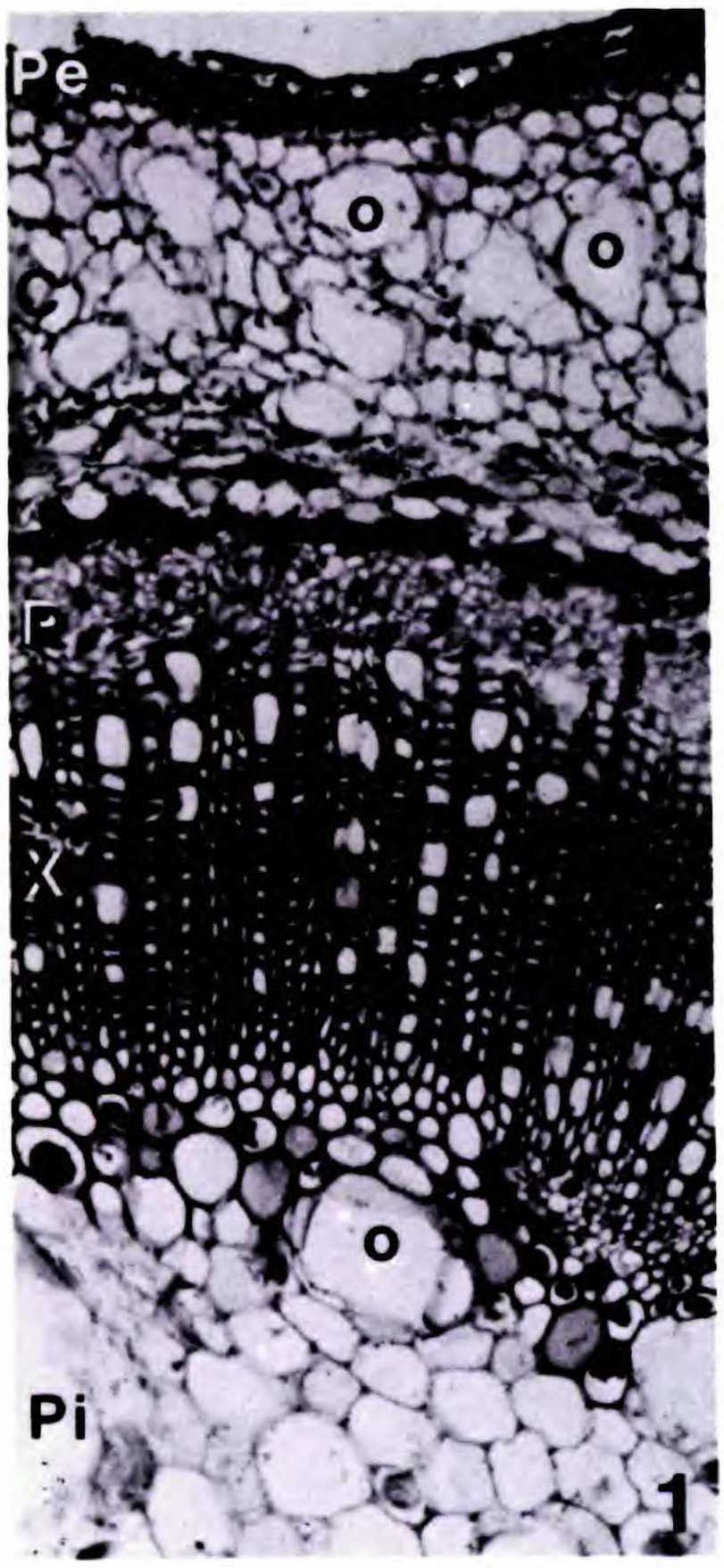

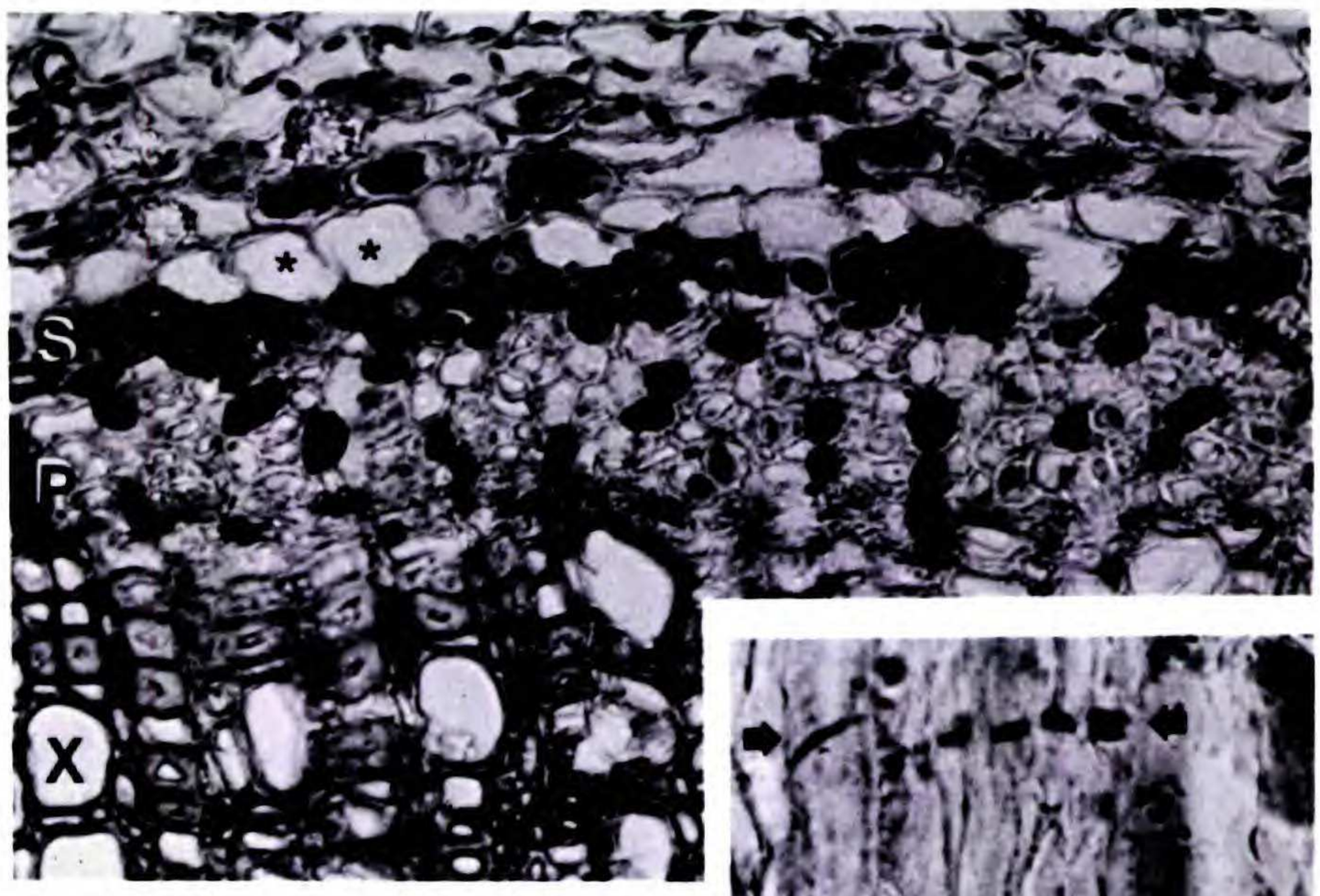

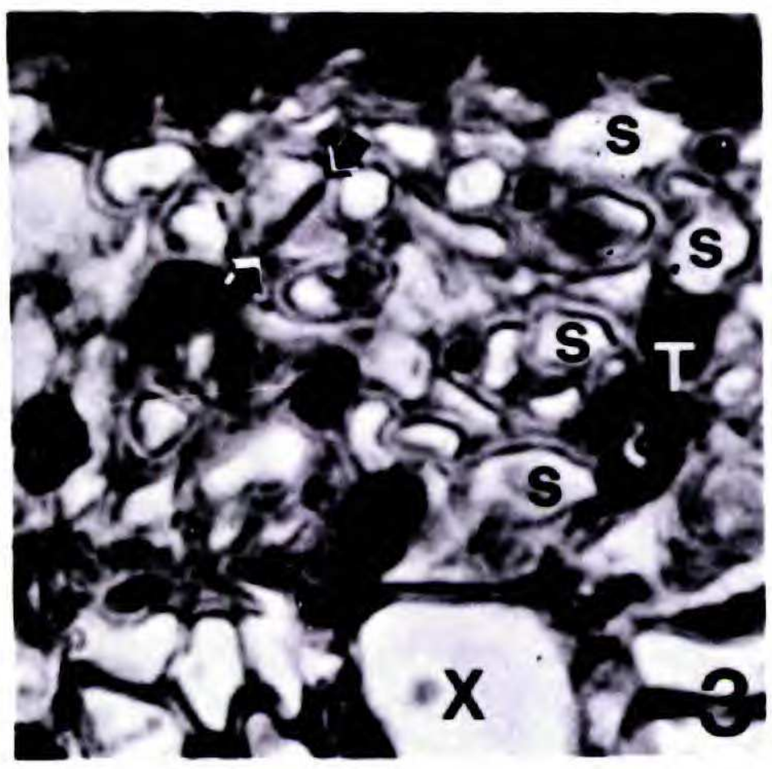

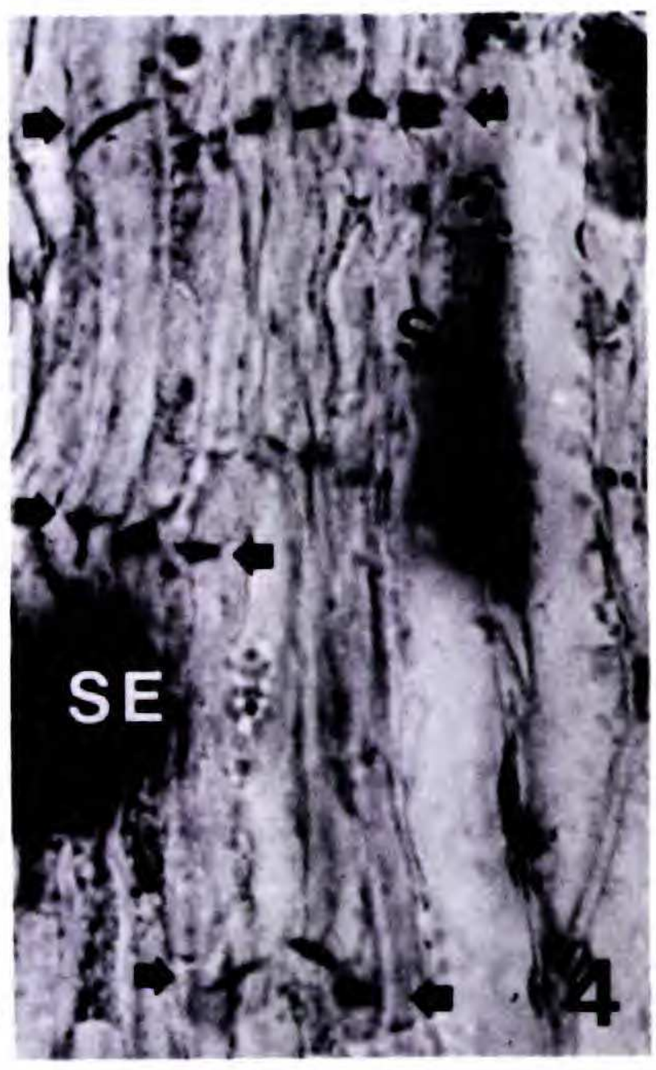

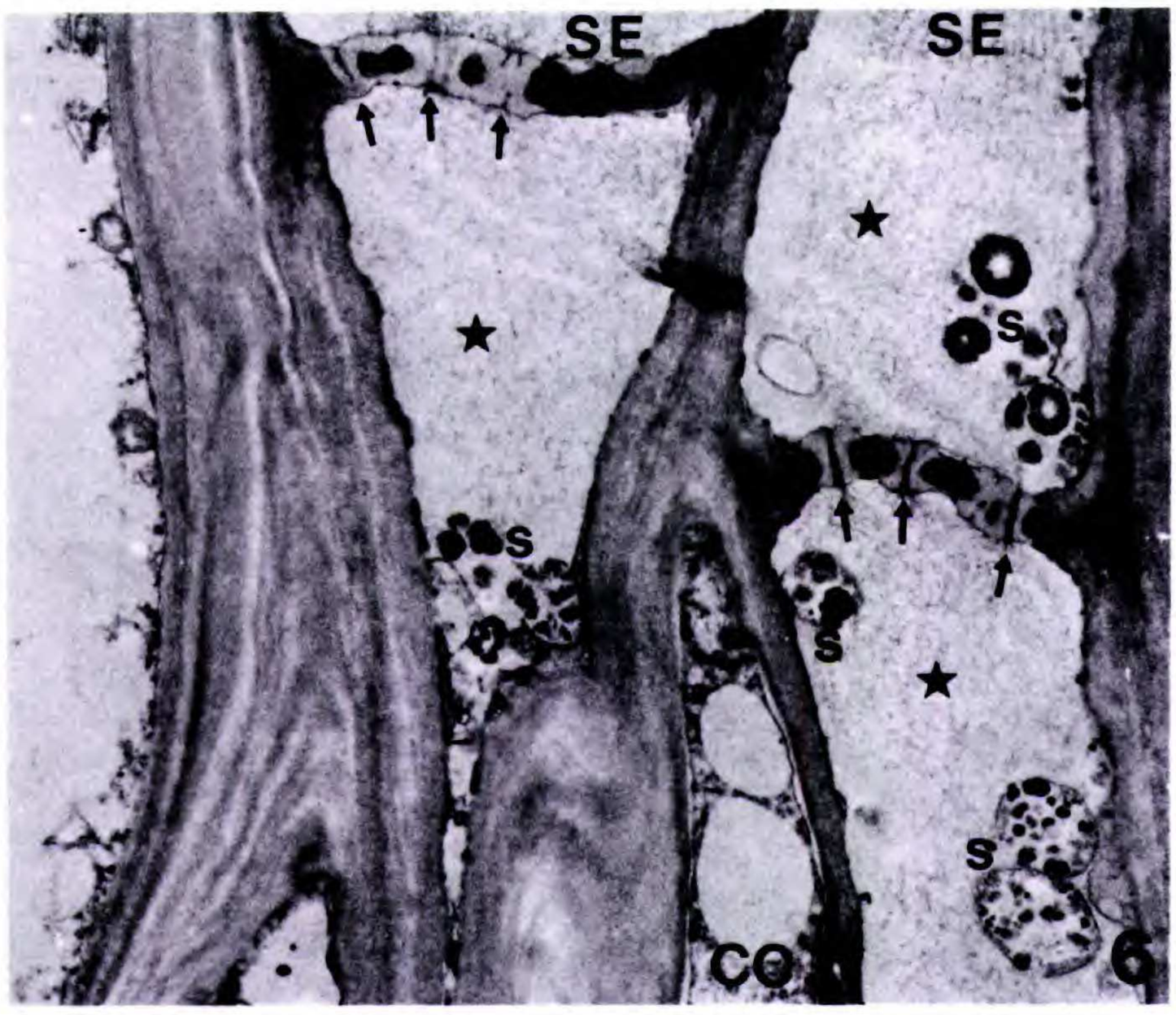

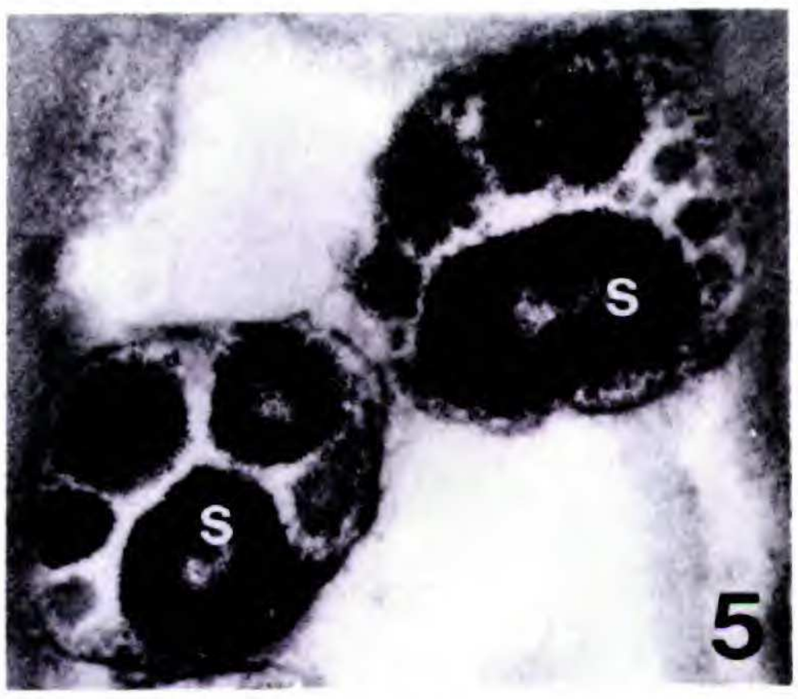

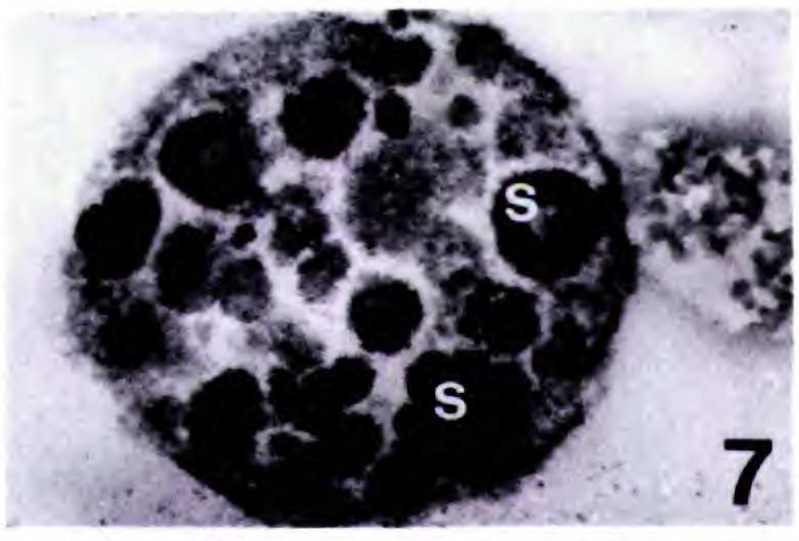

FIGURES 1–7. *Ticodendron incognitum*. — 1. Cross section of young shoot with periderm (Pe), cortex (C), phloem (P), xylem (X), and pith (Pi). Cortex and pith contain secretory elements (o); ×100. — 2. Detail of cross-sectioned vascular cylinder showing part of secondary xylem with vessels (X), phloem delimited against the cortex by sclerenchyma (S), and a pericycle made up of transparent cells (*); ×230. — 3. Part of cross-sectioned phloem with numerous thick-walled sieve elements (s) and black tannin cells (T); oblique sieve plate between arrows; ×500. — 4. Longitudinal section through phloem with many parallel-aligned sieve elements (SE) with sieve plates between arrows; ×570. — 5, 7. S-type sieve-element plastids with many small to medium-sized starch grains (s); ×30,000. — 6. TEM longitudinal

cambial initials. The cambial layer itself is rather small and difficult to delimit.

The sclerenchymatous sheath (Fig. 2: S) consists of mostly one layer of thick-walled fibers, but longitudinal sections indicate that thinner-walled stone cells do occur rather frequently, probably bridging the gaps between different fiber groups. A one-celled pericyclic layer of clear parenchymatic cells adjoins the sclerenchyma toward the periphery of the shoot (Fig. 2: *).

The cortex is composed of small parenchyma cells and numerous large secretory cells (Fig. 1: C, ○). Compared to the pith secretory sacs, these are much shorter, their extension being almost the same in all directions.

The content of the pith and cortex secretory elements seems to be mucilaginous. In addition, small cells containing tanninlike substances (Fig. 3: T) are frequently found in the cortex and are also present in all other tissues (see black cells in Figs. 1–3). Crystal cells (containing clustered crystals) are abundant in the cortex but are also frequent in the phloem and in the lignified pith cells, which border the innermost xylem.

Sieve-element Characters

The phloem of *Ticodendron* is composed of sieve elements (Fig. 3: s), companion cells (Fig. 6: CC), and phloem parenchyma cells. Comparatively many of the parenchyma cells, including those in phloem rays, contain tanninlike substances (Fig. 3: T)

With a diameter of 6–10 μm, sieve elements of *Ticodendron* are very narrow; their length is about 80–100 μm. Secondary sieve elements are somewhat smaller than primary ones and are more regularly aligned (see Fig. 4 with sieve plates aligned between arrows). Sieve plates are commonly restricted to the end walls and have their pores arranged in a single sieve area (simple sieve plate). The position of the sieve plate is in general at right angles to the lateral wall, and only in some cases is much inclined (Fig. 3, between arrows). The pore diameter is about 0.5 μm (Fig. 6, arrows), mostly occluded by heavy callose collars (due to unfavorable conditions during tissue preparation of the sample used).

As seen with the transmission electron microscope, sieve elements have comparably thick walls and are enucleate when mature. Plastids and mitochondria are about the only organelles present and reside at the periphery of the cells, whereas filaments of P-protein are dispersed throughout the sieve element (Fig. 6: ⋆) and are also trapped within the sieve pores.

The sieve-element plastids contain starch grains only and thus belong to the S-type. Their average diameter is about 1 μm, and they contain an average of eight round or ovoid starch grains. However, there is much size variation among *Ticodendron* sieve-element plastids (compare Figs. 5 and 7); diameters range from 0.7 to 1.5 μm.

No persistent or nondispersive P-protein bodies were found in the investigated sample. All mature sieve elements screened contained P-protein, the filaments of which were more or less evenly dispersed over the cell lumina (Fig. 6: ⋆).

Comparison of the *Ticodendron* Sieve-element Characters to Those of Putatively Related Taxa

The sieve elements of *Ticodendron* contain S-type plastids as do the great majority of dicotyledons, including all of the hamamelidalean families (Behnke, 1981a, 1989). The plastids of *Ticodendron* are smaller (1.0 μm) than the total average of S-type plastids (1.4 μm, based on 1,400 S-type species). The families that contain S-type plastids with an average diameter between 1.2 and 0.8 μm include 12 of the 28 families of putative hamamelid alliance, five of the six families making up the Fagales and all of those in the Urticales (Behnke, 1989).

Variation in the morphological features of the starch grains of *Ticodendron* falls outside that of the families of Urticales; their starch grains are larger and fewer (compare Figs. 6 and 7 with figs. 6.5 and 6.6 in Behnke, 1989). Also, with the exception of the Cannabaceae, all of the Urticales sieve elements contain a specific globular nondispersive P-protein body (see fig. 6.1 in Behnke, 1989), lacking in *Ticodendron*.

Among the families of Fagales, the Nothofagaceae differ by their larger-sized plastids and the Fagaceae by their compound-spherical nondispersive protein bodies found in all species studied so far. Betulaceae and/or Corylaceae would have the

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section through part of phloem with two sieve elements (SE) and a companion cell (CC). The sieve elements contain many S-type plastids (S) and evenly dispersed filaments of P-protein (⋆). Sieve pores (arrows) are almost totally occluded by callose deposits (white wall parts) and arranged into simple sieve plates; ×5,000.

closest similarities in their sieve-element characters. The Betulaceae s.l. (e.g., in the sense of Cronquist, 1981, or Takhtajan, 1987) have S-type plastids with an average diameter of 1.2 μm and about five medium-sized starch grains. If Corylaceae are held to be a separate family (e.g., Dahlgren, 1989), their plastid characters (diameter 1.1 μm; about eight starch grains) would fit nicely with those of *Ticodendron*. However, considering the comparatively wide range of measurements on which averages are based, none of the discussed families would seem inappropriate.

Based on its sieve-element data, *Ticodendron* would fit best within Betulaceae/Corylaceae, if only hamamelid families are considered. It is obvious that a positive alignment of *Ticodendron* cannot be given on only sieve-element characters; these characters can only be used to favor or exclude proposals for a taxonomic position made on account of many other characters.

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